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Source: Tropical Conservation Science, 10(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082917702651

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Research Article

Tropical Conservation Science
Volume 10: 1–12
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sagepub.com/journalsPermissions.nav
DOI: 10.1177/1940082917702651
journals.sagepub.com/home/trc

The Role of Mountains as Refugia for Biodiversity in Brazilian Caatinga: Conservationist Implications

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Abstract

The relationship between how humans and altitude influence the structure of plant communities has been poorly investigated and particularly so in semiarid ecosystems. Understanding the processes that affect plant community structure is essential for sustaining the biodiversity found in altitudinal refugia of the Brazilian Caatinga. In this study, we investigated the influence of altitudinal gradients and human impacts on floristic composition and structure of a shrubby-arboreal community in northeastern Brazil. We recorded a total of 68 tree species in 45 randomly sampled 4×50 m plots in three different altitudinal levels (Level 1, Level 2, and Level 3). The species clearly separated among the altitudes studied when the abundance data were analyzed (Bray–Curtis, Nonmetric Multidimensional Scaling). Whittaker plots indicated that Level 3 (highest) had more species and greater evenness and thus greater diversity. On the other hand, Level 1 (lowest) had lower diversity with greater dominance of a few pioneer species. Our results indicated that higher altitudes appear to function as refugia for many plant species (unique species and species shared with Atlantic Forest), which results in greater specie richness. However, high levels of human disturbance at lower altitudinal levels contribute to lower diversity due to the competitive abilities and dominance of pioneer tree species. The maintenance of these altitudinal Caatinga refugia is important and should be a priority for the implementation of new protected areas in the semiarid region of Brazil.

Keywords

Brazilian semiarid, elevation gradient, mountain range, land use intensification

Species composition and community structure are modulated by different microhabitats (Walther et al., 2002; Wiegmann & Waller, 2006). Therefore, environmental gradients (Bernard-Verdier et al., 2012), particularly elevation gradients, in which environmental changes can influence floristic composition and genetic diversity, must been studied (Boulangeat, Lavergne, Van, Garraud, & Thuiller, 2012). On the other hand, human activities have had a marked effect on biodiversity patterns (Kessler, 2009; Rahbek, 1995), with land use intensification having the greatest negative effect on species richness and causing changes in ecosystem processes (Hooper et al., 2012). Therefore, it is important to identify and conserve refugia that sustain high levels of biodiversity, particularly for semiarid ecosystems (Manhães, Mazzochini, Oliveira-Filho, Ganade, & Carvalho, 2016).

One evident feature of the Brazilian semiarid region is the presence of mountains that are less than 1,000 meters in altitude (Instituto Brasileiro de Geografia e Estatística [IBGE], 2012). These mountains are natural barriers to human exploitation and accessibility and possess a more humid climate (mesic environment) than the surrounding landscape and thus serve as the

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Received 12 December 2016; Revised 22 February 2017; Accepted 23 February 2017

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refugia for biodiversity (Ribeiro, Rodríguez, Santos, Tabarelli, & Leal, 2015; Silva, Lopes, Lopez, Melo, & Trovão, 2014). This pattern of diversity is typical of Brazilian semiarid mountains but is unlike the pattern of decreasing biodiversity with increasing altitude found in other mountainous regions of the world (Nogués-Bravo, Araújo, Romdal, & Rahbek, 2008; Sanchez, Pedroni, Eisenlohr, & Oliveira-Filho, 2013; Toledo-Garibaldi & Williams-Linera, 2014).

The Caatinga (a seasonally dry tropical forest) is a typical semiarid ecosystem of Brazil. It is characterized by prominent seasonal rainfall with several months of severe drought (ranging from 240 to 1500 mm per year, with 5 to 6 months receiving <100 mm; Pennington, Lavin, & Oliveira-Filho, 2009) and high rates of potential evapotranspiration (1,500 a 2,000 mm per year; Moro, Lughadha, de Araújo, & Martins, 2016). Caatinga vegetation is comprised of deciduous trees and shrubs with anatomical, morphological, and functional adaptations determined by the adverse climatic and soil conditions present of the region (Pennington et al., 2009). The phytogeographical domain of the Caatinga borders other important tropical domains, including the Atlantic Forest to the east, the Amazon Forest to the west, and the Cerrado to the south, which has resulted in numerous shared ecological and floristic characteristics (Leal, Silva, Tabarelli, & Lacher, 2005; Moro et al., 2016).

Since colonial times, the forest of the Caatinga has been exploited for logging, agriculture, and grazing (Leal et al., 2005; Pereira, Andrade, Sampaio, & Barbosa, 2003), and local communities have long used its plants for a variety of different purposes (Lucena, Albuquerque, & Araújo, 2007; Lucena, Medeiros, Araújo, Alves, & Albuquerque, 2012; Lucena et al., 2013). These activities have homogenized the habitat, resulting in the loss of diversity and changes to the structure of plant communities (Albuquerque et al., 2012; Büchi & Vuilleumier, 2014; Ribeiro, Rodríguez, Souza, & Leal, 2016; Smart et al., 2006). In some ecosystems, such as low altitudinal areas of semiarid mountains, species richness can decrease as a result of the introduction of generalist species that can better withstand anthropogenic disturbance (Alexander et al., 2011).

Assuming that biodiversity is directly related to both environmental factors and human disturbance, we sought to determine whether the floristic composition and structure of shrub-arboreal communities differ along an altitudinal gradient in the semiarid Brazilian Caatinga. We expect that mountains of semiarid have greatest biodiversity and unique species due a more humid climate, making possible the occurrence of typical species of the Atlantic Forest. In addition, the lowest altitudinal levels have minor biodiversity due anthropogenic disturbance.

Method

Study Area

Fieldwork was conducted on Bodocongó mountain (07° 27′ 6″ S; 35° 59′ 41″ W), which is located in the municipality of Queimadas in the state of Paraíba, Brazil (Figure 1). The area lies within the Cariri Oriental microregion of the Brazilian semiarid region (Agência Executiva de Gestão das Águas do Estado da Paraíba [AESA], 2006).

The Cariri microregion is the driest area in Brazil and, according to the newly updated Köppen–Geiger classification system (Alvares, Stape, Sentellhas, Gonçalves, & Sparovek, 2013), its climate is classified as BSwh’, being warm and semiarid, with a dry season lasting 9 to 10 months and less than 300 mm mean annual rainfall (AESA, 2006). Temperature is variable, with a monthly minimum of 18°C to 22°C in July and August and a monthly maximum of 28°C to 31°C in November and December. The monthly mean relative humidity is 60% to 75%, reaching the maximum generally in June and the minimum in December (Bioclimatic variables, 2010).

The predominant vegetation is typical of semiarid regions in Brazil and consists of savanna physiognomies with endemic flora (Caatinga). It is characterized by shrubs and low trees with many with thorns, microphylls, and numerous xerophytic features (IBGE, 2012; Prado, 2008). The predominant soils in the region are classified as luvisol, neosol, and vertisol (Empresa Brasileira de Pesquisa Agropecuária, 2006).

The study was conducted on private property, which had clear signs of human impacts including selective logging and man-made trails. The intensity of human disturbance differed with altitude; at the lower altitudes, where human and animal access appeared to be possible, there was significant human disturbance (Silva et al., 2014). At the base of the mountain, there were many anthropogenic clearings; while at midaltitudes, there appeared to be less human impact, as indicated by the presence of primary vegetation (closed shrub-arboreal savanna). Individual shrubs and trees with greater basal area and height were commonly found at midaltitudes. The highest altitudes were difficult to access and appeared to have been minimally impacted; there were a few trails and marginal evidence of selective logging. The area surrounding the study site was a matrix of pasture, abandoned land in various states of regeneration, and agricultural crops.

Data Collection

We used the sampling methods proposed by Braun-Blanquet (Martins, 1989), and based on previous studies in mountain ranges in the Brazilian semiarid region (Carvalho, Souza, & Trovão, 2012; Oliveira, Trovão,

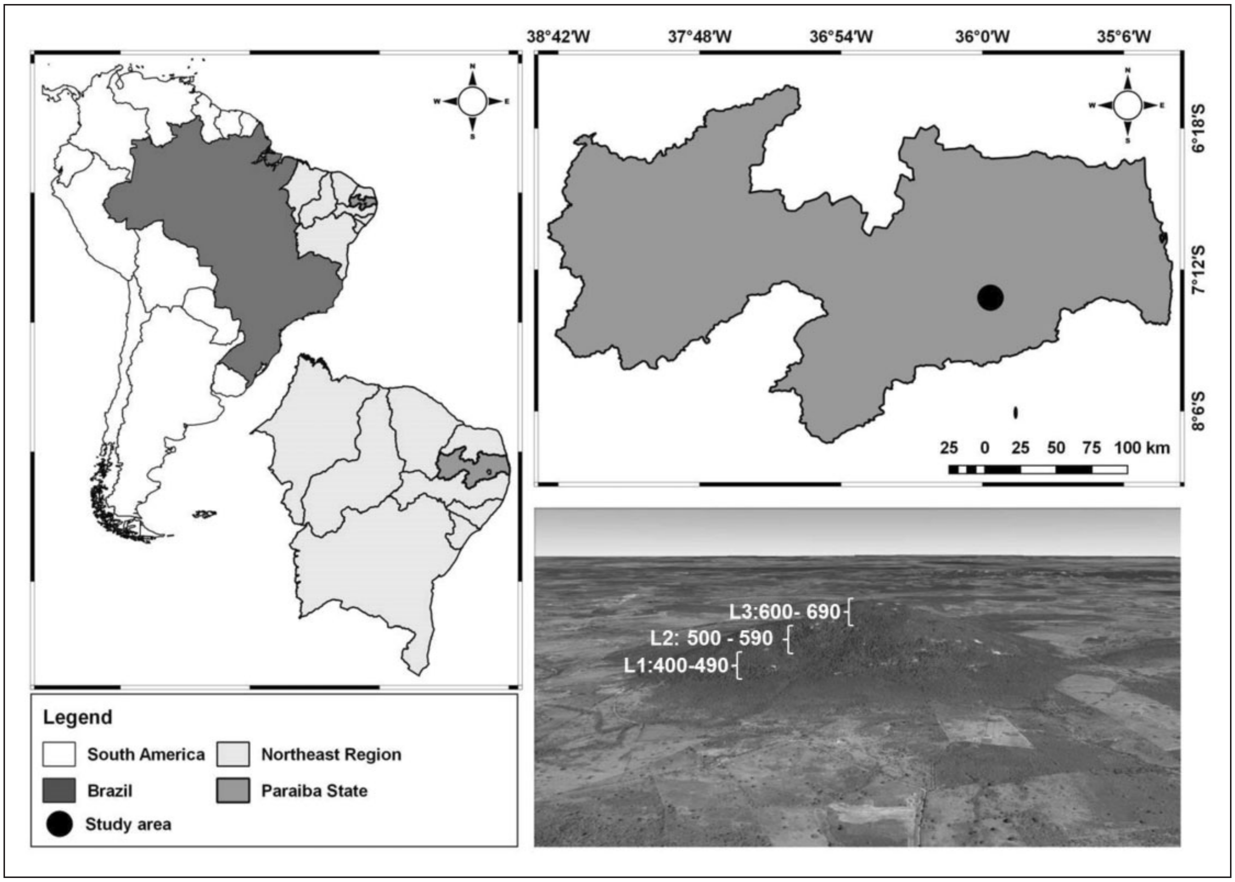

Figure 1. Location of the study area, Bodocongó mountain, municipality of Queimadas, state of Paraíba, in the semiarid region of Brazil. Altitudinal levels and the matrix of agriculture and livestock areas surrounding the mountain are shown in detail.

Souza, & Ferreira, 2009; Silva et al., 2014), plots were distributed at three different altitudes throughout the altitudinal gradient using a Garmin Global Position System (GPS). The three altitudinal levels reflected homogeneous sample domains and consisted of the following: L1 400 to 499 m (Level 1, base of the mountain), L2 500 to 599 m (Level 2, midaltitude), and L3 600 to 690 (Level 3, maximum altitude) (Figure 1). Fifteen random plots (without systematization) were sampled at each altitudinal level, totaling 45 plots (50 m × 4 m) and a total of 1 ha.

In each plot, all live arboreal shrubs with ground-level stem diameters of $\geq$3 cm and heights of $\geq$1 m were sampled (Rodal, Sampaio, & Figueiredo, 2013). We used calipers and a tape measure to measure plant diameter; for individuals with multiple stems, each stem was measured individually. Plant height was measured using a 12 -m long stick subdivided at every 2 m. For unidentified species, vegetative parts were collected and identification was performed at Manuel de Arruda Câmara, Universidade Estadual da Paraíba, Campus I, Campina Grande, or by a third-party specialist. All scientific names were verified by specialists following the Missouri Botanical Garden (www.mobot.org) and the Northeast Center for Plant Information databases (www.cnip.org.br). The Angiosperm Phylogeny Group IV (APG IV) classification system (APG, 2016) for the family- and genus-level nomenclature was used.

Statistical Analyses

In order to document spatial variation of the plant communities along the altitudinal gradient, Nonmetric Multidimensional Scaling (MDS) was applied to square-root transformed abundance data using Bray–Curtis distance and a stability criterion of 0.00001 in order to obtain the best two-dimensional description of the data set (McCune & Grace, 2002). MDS is considered an efficient technique for ordination of ecological samples based on species occurrence (McCune & Mefford, 2011). The suitability of the ordination was assessed by the stress value, which indicates the relationship between the Euclidean distance among samples relative to the ordination axis. Bray–Curtis dissimilarity was used to determine the floristic compositional distances. Overall, the MDS was used to investigate changes in community composition and the formation of subgroups along the altitudinal gradient. Stress values on MDS plots below 0.2 are an indication of a good fit (Borcard, Gillet, & Legendre, 2011).

Next we used a permutational multivariate analysis of variance (PERMANOVA) with 9,999 random permutations (Anderson, 2001) to test if the groups segregated by MDS were significant. To test for any dispersion effect, a Permutational test of dispersion (PERMDISP) was also performed to check for homogeneity of the multivariate dispersions considering the compositions of each altitudinal level. A nonsignificant PERMDISP test would indicate that any significant result obtained in the PERMANOVA was a result of a location effect (higher or lower average size composition). To identify the species that had the greatest contribution to similarity within levels, and dissimilarity among levels, we used an analysis of similarity percentage breakdown (SIMPER). As a result, only five species represented the most influential species of each group. All analyses were performed using PRIMER-E software with the PERMANOVAÞ add-on package (Anderson, Gorley, & Clarke, 2008).

Variables of community structure, including richness, density (ha^{-1}), basal area (ha^{-1}), diameter, and average height were analyzed for each altitudinal level using the program FITOPAC Shell, Version 2.1 (Shepherd, 2010). In order to meet the assumptions of normality and homoscedasticity, the data (response variables) were tested using Shapiro–Wilk test and subsequently transformed and standardized (Hammer, Harper, & Ryan, 2001). An ANOVA was then used, with a Tukey post hoc test (confidence level of 95%, $p < .05$) to compare response variables using the Paleontological Statistics program—PAST 2.17 c (Hammer et al., 2001).

We calculated the Shannon diversity index (H') and the evenness (J') for each altitudinal level using the program PAST 2.17 c (Hammer et al., 2001). A Hutcheson's *t* test was performed in order to better compare the diversity index values calculated for each altitudinal level using the software PAST 2.17 c. In order to visualize the distribution of the abundance of each species, a Whittaker's plot was constructed with log-transformed species abundance data. A Spearman's rank correlation analysis was used to assess the relationship between altitude and the community response variables (richness, density, basal area, diameter, and average height).

Results

A total of 68 species/morphospecies (2,808 individuals and 20 families) were sampled (Appendix). The mountain has a floristic unit, with over 50% of total species distributed along of the three altitudinal levels; but in terms of abundance, the MDS showed a clear separation among the levels (Figure 2). The ordination had a stress value of 0.2 indicating that it adequately separate the samples along the altitude gradient. The three altitudinal levels were significantly different in terms of their composition and abundance along the gradient—PERMANOVA, $Pseudo\text{-}F_{2,44} = 6.676$; 0.01. The average distance to the group centroid based on assemblage dissimilarities (i.e., species turnover or β diversity) also differed among the levels (*PERMDISP*, $F_{2,42} = 11.24$; 0.01). Altitudinal level L3 had the highest average distance to the group centroid (0.49) followed by L2 (0.39) and L1 (0.37).

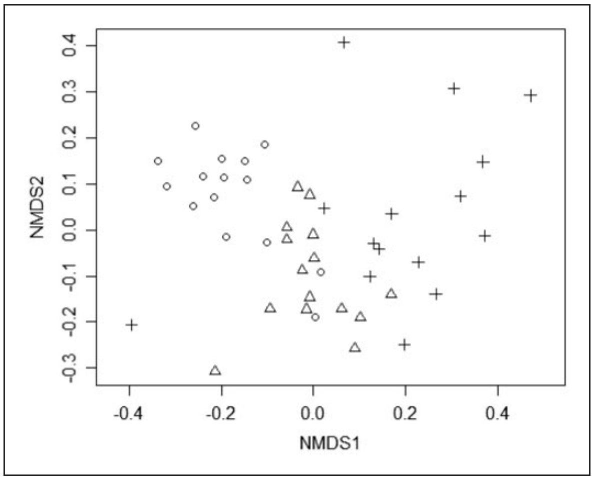

Figure 2. Floristic groups corresponding to the altitudinal level in the mountain of Bodocongó in the semiarid region of Brazil. The samples (plots) are ordered for each of the two dimensions of a nonmetric multidimensional ordination performed using site abundance-based Bray–Curtis similarity matrix and altitude (see Method section for details). Circles are the L1 plots, triangles are the L2 plots, and crosses are the L3 plots.

The SIMPER analysis indicated 45.5% similarity among taxa of the first level, 42.68% similarity among the L2 samples, and 28.46% similarity among the L3 samples (Table 1). The plants that contributed to the similarity of each level and dissimilarity among levels are shown in Table 1.

Species richness for levels ranged from 38 to 55 (Table 2). The number of unique species was greatest in L3 (10) and much lower in L1 (only *Sideroxylon obtusifolium,* Sapotaceae) and L2 (two species; Morphospecies VII and *Pilosocereus gounellei,* Cactaceae). The Whittaker's plot showed that L3 had more species (longer tail) and more evenness (curve with the most gradual inclination) than the other two elevation levels (Figure 3). This pattern reflects greater diversity in L3, although the three altitudinal levels had significantly different Shannon–Wiener indices (Table 2). Altitudinal level L1 had lower richness and diversity due to greater dominance of two species (Figure 3), *Croton blanchetianus* (Euphorbiaceae) and *Poincianella pyramidalis* (Fabaceae), which together represented 58.8% of the total plant abundance of this level.

Table 1. The Influential Species That Most Contributed to Similarity Within the Levels and Dissimilarity Among the Levels (SIMPER Results).

Levels	L1	L2	L3
L1	45.50%		
	Croton blanchetianus (Euphorbiaceae)		
	Poincianella pyramidalis (Fabaceae)		
	Aspidosperma pyrifolium (Apocynaceae)		
	Mimosa ophthalmocentra (Fabaceae)		
	Piptadenia stipulacea (Fabaceae)		
L2	68.15%	42.62%	
	Croton blanchetianus (Euphorbiaceae)	*Allophylus puberulus* (Sapindaceae)	
	Poincianella pyramidalis (Fabaceae)	*Commiphora leptophloeos* (Burseraceae)	
	Allophylus puberulus (Sapindaceae)	*Bauhinia cheilantha* (Euphorbiaceae)	
	Piptadenia stipulacea (Fabaceae)	*Aspidosperma pyrifolium* (Apocynaceae)	
	Bauhinia cheilantha (Euphorbiaceae)	*Sapium glandulosum* (Euphorbiaceae)	
L3	79.33%	69.60%	28.46%
	Croton blanchetianus (Euphorbiaceae	*Allophylus puberulus* (Sapindaceae)	*Allophylus puberulus* (Sapindaceae)
	Poincianella pyramidalis (Fabaceae)	*Bauhinia cheilantha* (Euphorbiaceae)	*Manihot glaziovii (*Euphorbiaceae)
	Allophylus puberulus (Sapindaceae)	*Clusia paralicola* (Clusiaceae)	*Bauhinia cheilantha* (Euphorbiaceae)
	Piptadenia stipulacea (Fabaceae)	*Poincianella pyramidalis* (Fabaceae)	*Clusia paralicola* (Clusiaceae)
	Clusia paralicola (Clusiaceae)	*Croton heliotropiifolius* (Euphorbiaceae)	*Croton blanchetianus* (Euphorbiaceae)

Note. Just five species represented the most influential species of each group.

Table 2. Structural Variables of the Three Altitudinal Levels of the Mountain Studied in Semiarid Brazil.

Structural variables	Level 1	Level 2	Level 3
Families	18	20	21
Richness	38	50	55
Chao 1	38.6	55.1	60.0
Unique species	1	2	10
Shannon–Wiener index (H′)	2.265^{c}	3.081^{b}	3.209^{a}
Pielou evenness index (J′)	0.623	0.788	0.801
Abundance per plots	$81.93\ (\pm\ 28.29)^{a}$	$55.0\ (\pm\ 14.92)^{b}$	$49.71\ (\pm\ 17.84)^{b}$
Density (ind/ha)	$2.74\ (\pm\ 1.01)^{a}$	$1.92\ (\pm\ 0.53)^{b}$	$1.85\ (\pm\ 0.54)^{b}$
Basal Area (m^2/ha)	$0.51\ (\pm\ 0.19)^{a}$	$0.64\ (\pm\ 0.31)^{a}$	$0.37\ (\pm\ 0.20)^{b}$
Average diameter (cm)	$7.55\ (\pm\ 1.88)^{b}$	$9.5\ (\pm\ 1.77)^{a}$	$6.92\ (\pm\ 2.12)^{b}$
Average height (m) ns	3.84 (± 1.56)	5.35 (± 1.22)	4.32 (± 1.61)

Note. Values between parentheses are standard deviation. *ns* = nonsignificance.
[a,b,c]Different letters mean significant difference between the averages for each trait ($P < 0.05$), from post hoc Tukey test groupings.

From a total of 68 species, 31 species were sampled in all three levels but with varying abundances along the altitudinal gradient. *Handroanthus impetiginosus* (Bignoniaceae) and *Talisia esculenta* (Sapindaceae) represented 90% and 76% of the total number of individuals measured in L3, respectively. Similarly, some species were more abundant in L2 than in other levels, for example, *Aspidosperma pyrifolium,* Apocynaceae (45% of individuals of the species), *Commiphora leptophloeos,* Burseraceae (73%), *Sapium glandulosum,* Euphorbiaceae (91%), and *Allophylus puberulus,* Sapindaceae (77%; Figure 4).

In relation to the response variables, abundance (number of individuals) and density varied significantly, $F_{2,44} = 9.784$ and $F_{2,44} = 7.691$; $p < .01$, respectively, with average values of 49.7 to 81.9 individuals and 1.85 to 2.74

individuals/ha per level, respectively (Table 2). For both variables, the greatest values were encountered in L1. Basal area varied significantly among the levels, $F_{2,44} = 7.899$; $p < .01$; however, the Tukey test only indicated that L3 was statistically different, while L1 and L2 had similar values. The similar values of basal area for L1 and L2 can be attributed to different causes, since L1 had higher plant density while L2 had larger diameter and height values due to the presence of larger individuals (Table 2).

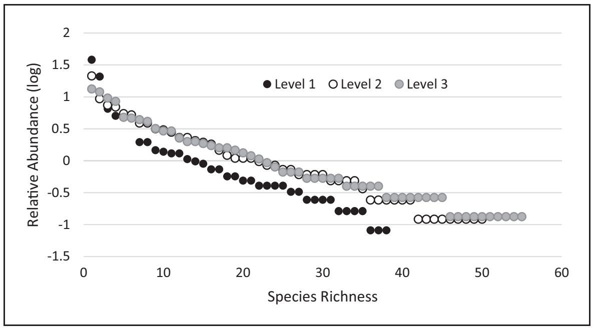

Figure 3. Whittaker's plot (or dominance plot) for the three altitudinal levels of the Bodocongó mountain in the semiarid region of Brazil. Level 3 has more species (curve with the longest tail) and more evenness (curve with most gradual inclination) than the other two altitudinal levels. Altitudinal Level 1 has the fewest species but the highest dominance.

A negative correlation was found between altitude and density ($r_s = -.522$; $p < .01$) and altitude and basal area ($r_s = -.33$; $p < .05$). However, a positive relationship was found between diversity and altitude ($r_s = .335$; $p < .05$).

Discussion

The results presented here indicate that the plant communities on Bodocongó mountain are significantly different in terms of flora, abundance, basal area, diversity, and evenness. Changes in plant composition and diversity along a gradients have been observed in other studies (Sagar, Raghubanshi, & Singh, 2003; Smart et al., 2006; Ribeiro et al., 2016). The high density, low richness, low diversity, and low evenness values at L1 (base of the mountain) appears that is common landscape of the Brazilian Caatinga (typical Caatinga), which is nationally recognized as a highly fragmented and human-impacted ecosystem (Gariglio, Sampaio, Cestaro, & Kageyama, 2010; Leal et al., 2005; Ramos, Ramos, & Albuquerque, 2012; Ribeiro et al., 2016). The use and occupation of the Brazilian Caatinga has caused numerous changes to the composition and structure of the vegetation (Pereira, Andrade, Costa, & Dias, 2001; Ribeiro et al., 2015; Ribeiro et al., 2016). The extensive conversion of natural areas to human-modified landscapes is currently the most significant threat to this ecosystem (Araújo et al., 2010; Carmel & Kadmon, 1999; Quesada et al., 2009; Ribeiro et al., 2016). Human disturbance has enabled increased dominance by some species (Ribeiro et al., 2016; Smart

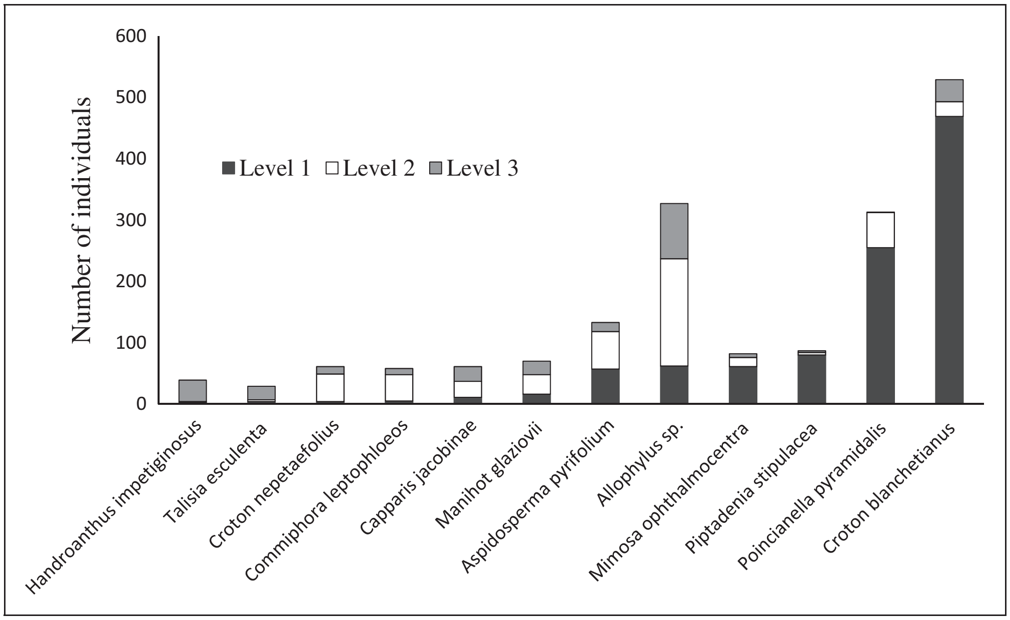

Figure 4. Differences in the number of individuals of the 12 most abundant species sampled among the three altitudinal levels (L1, L2, and L3) of the Bodocongó mountain in the semiarid region of Brazil. The level of greatest abundance varies among species and the most abundant species are present in L1.

et al., 2006) and consequently can reduce basal area, average height, and evenness of a plant community (Ramirez-Marcial, Gonzalez-Espinosa, & Williams-Linera, 2001; Virtanen et al., 2010; Wiegmann & Waller, 2006).

In disturbed areas, successful pioneer tree species can dominate the environment by limiting the development of species less tolerant to these environmental conditions (Büchi & Vuilleumier, 2014; Ribeiro et al., 2016). In many situations, taxonomic impoverishment of tropical plant assemblages is associated with the extirpation of key ecological plant groups (e.g., old growth flora; loser species) (Leal, Andersen, & Leal, 2015) or the proliferation of particular lineages resulting in the cooccurrence of more closely related taxa (Ribeiro et al., 2016). Following this, few winners among the original tree species remain (Zhao, Pan, Tan, & Corlett, 2015), thus functional diversity is reduced (Tabarelli, Lopes, & Peres, 2008).

C. blanchetianus and *P. pyramidalis* are abundant and in high densities in forests following long periods of exploitation (Carvalho et al., 2012; Sampaio, 1995; Stanley, Voeks, & Short, 2012). In one review of 131 surveys, these species were considered to be the most common woody species found throughout the Caatinga Phytogeographical Domain (Moro et al., 2016). In the present study, these species were found in high density in Level 1. Furthermore, only one unique species was sampled in L1 (Table 2). Human disturbance at the base of the mountain could have affected the presence of rare species (species with 1–5 individuals; Saiful & Latiff, 2014) and unique species (Bhat et al., 2000), and overall could have impoverished the plant community (Ribeiro, et al., 2016; Zhang, Cheng, Zang, & Ding, 2014).

On the other hand, the medium to high diversity values ($H' > 3.1$) found in L3 resemble those found in seasonal dry forests (Cestaro & Soares, 2004; Lopes, Schiavini, Oliveira, & Vale, 2012; Lopes, Schiavini, Vale, Prado-Júnior, & Arantes, 2012; Prado-Júnior et al., 2016). These results indicate a significant increase in diversity along the altitudinal gradient ($r = .335$; $p < .05$). This finding was expected, since mountains (or mountain ranges) of the semiarid region are considered to be biodiversity refugia in relation to the surrounding matrix not only because provide natural protection from human disturbance, especially at the highest elevations (Silva et al., 2014), but also because plant community of the top of these mountainous are a mix of Caatinga species and Atlantic Forest species (Carnaval, Hickerson, Haddad, Rodrigues, & Moritz, 2009; Carnaval & Moritz, 2008; Leite et al., 2016; Werneck, Costa, Colli, Prado, & Sites, 2011).

According to forest refuge hypothesis, the Atlantic Forest of eastern South America probably expanded its area in a wetter period in the past and then retracted during the last glacial maximum (Werneck et al., 2011) and would have promoted reproductive isolation and consequently ecological refuges surrounded by open habitats (Prance, 1982). Thus, the vegetation of the Caatinga refugium may have differed structurally across Quaternary fluctuations enabling the growth of semideciduous forest in areas that currently support dry shrub-arboreal communities (Auler et al., 2004).

Some results found in this study corroborate this hypothesis as they also found that higher altitudes have more unique species (several which occur at the Atlantic Forest; Werneck et al., 2011) and that plant composition at lower altitude is similar to the typical Caatinga vegetation found in other sites (Ribeiro et al., 2016; Smart et al., 2006).

The wetter climate at the highest elevations allowed the persistence of tropical forest species inside Caatinga boundaries. The mountains of the Brazilian semiarid region are wetter ecosystems than the typical Caatinga in the region, where the hydric balance is more stable and mild temperatures and lower evaporation rates are persistent; this, in turn, leads to the development of a diverse plant community (Sampaio, 2010; Silva et al., 2014). An example of this includes the presence of *Clusia paralicola* G. Mariz (Clusiaceae) in L2, which contributed to the increased density of this level due to the high basal area of this species. *C. paralicola* is typical of wet environments (Alcoforado-Filho, Sampaio, & Rodal, 2003) and until now had not been sampled in mountains of the semiarid region of Brazil (i.e., first record). Limited dispersal to favorable microhabitats can cause specific conditions where species are exclusively found in only a few locations (Born et al., 2014; Kraft et al., 2015). Nevertheless, the theory of nonequilibrium can also cause the isolate occurrence of some species (Reice, 1994). If the climate is historically changing (Werneck et al., 2011), an isolated individual from one rare species could be a relict from a population that is going regionally extinct.

Implications for Conservation

Our results indicate that mountains of the Caatinga represent a landscape feature that can sustain higher levels of diversity, functioning as refugia for many plant species, and subsequently increasing species richness. These refugia are the result of limited physical accessibility for human disturbance and a more humid climate (mesic environment) than the surrounding matrix. In addition, the mountain tops can be a relict vegetation (refugia) of an ancient Humid Tropical Forest that expanded its area in a wetter period in the past and retracted after drying climate, resulting in higher levels of genetic diversity and endemism (Queiroz, 2006). On the other hand, human disturbance at the base of the mountain has resulted in taxonomic impoverishment and changed the structure of resident plant communities.

The maintenance of these refugia should be the top priority of establishment of new protected areas (PAs) in the Brazilian semiarid ecosystem. The mountains of the Brazilian Caatinga need to be protected from the strong anthropogenic pressures to which they have already been subjected. The vegetation of the Caatinga is found in only 1.1% of the current PAs (Hauff, 2010). These mountains are extremely relevant for the creation of new PAs. The results provided here highlight the importance of considering these zones as possible areas for protection by the Brazilian government. Adequate conservation efforts should prevent the advancement of human disturbance to other levels of the mountain (middle and high altitudes), and conservation strategies promoting Caatinga biodiversity should, whenever possible, prioritize the maintenance of the mountain as a whole.

Efforts should not be limited to creating PAs (conservation units) but also directed toward the conservation of managed areas and their local populations (Manhães et al., 2016), as a comanagement system (resource users and governmental agencies), motivating humans to conserve. Finally, it is necessary to understand that plant use by local communities is an integral part of the ecosystem and may be reflected in the structure of plant communities.

Appendix

Table A1. List of Species With Respective Numbers of Individuals and Basal Area Per Level Altitudinal in Mountain Studied in Semiarid Brazil.

	Level 1		Level 2		Level 3	
Species (family)	NI	BA	NI	BA	NI	BA
Croton blanchetianus (Euphorbiaceae)	469	1.702	24	0.127	36	.157
Poincianella pyramidalis (Fabaceae)	255	1.434	57	0.446	1	.002
Allophylus puberulus (Sapindaceae)	62	0.189	175	1.189	90	.415
Piptadenia stipulacea (Fabaceae)	80	0.500	4	0.053	3	.013
Bauhinia cheilantha (Euphorbiaceae)	24	0.087	77	0.333	72	.254
Croton heliotropiifolius (Euphorbiaceae)	24	0.111	32	0.17	64	.201
Mimosa ophthalmocentra (Fabaceae)	61	0.471	15	0.121	6	.018
Aspidosperma pyrifolium (Apocynaceae)	57	0.498	61	1.018	15	.329
Sapium glandulosum (Euphorbiaceae)	4	0.058	45	0.541	12	.09
Commiphora leptophloeos (Burseraceae)	5	0.176	43	0.662	10	.251
Handroanthus impetiginosus (Bignoniaceae)	3	0.039	1	0.008	35	.272
Manihot glaziovii (Euphorbiaceae)	16	0.084	32	0.14	22	.102
Capparis jacobinae (Capparaceae)	11	0.041	26	0.074	24	.076
Myracrodruon urundeuva (Anacardiaceae)	18	0.384	23	0.466	9	.162
Talisia esculenta (Sapindaceae)	4	0.03	3	0.056	22	.089
Jatropha molissima (Euphorbiaceae)	12	0.031	19	0.042	3	.004
Pseudobombax marginatum (Malvaceae)	3	0.016	19	0.281	4	.097
Anadenanthera colubrina var. *colubrina* (Euphorbiaceae)	17	0.773	4	0.198	1	.001
Morphospecies 1	16	0.048	7	0.028	3	.005
Pilosocereus glaucescens (Cactaceae)	7	0.044	16	0.203	12	.175
Schinopsis brasiliensis (Anacardiaceae)	9	0.386	9	0.611	15	.276
Acalypha multicaulis (Euphorbiaceae)	5	0.009	6	0.017	14	.031
Cynophalla flexuosa (Capparaceae)	5	0.045	10	0.225	13	.063
Lantana microphylla (Verbenaceae)	6	0.015	12	0.123	4	.032
Cereus jamacaru (Cactaceae)	9	0.43	5	0.085	1	.115
Libidibia ferrea (Fabaceae)	6	0.026	9	0.409	2	.017
Ceiba glaziovii (Malvaceae)	3	0.088	8	0.458	2	.178

(continued)

Table A1. Continued

	Level 1		Level 2		Level 3	
Species (family)	NI	BA	NI	BA	NI	BA
Mimosa malacocentra (Fabaceae)	3	0.011	5	0.267	5	.03
Eugenia sp. (Myrtaceae)	1	0.004	4	0.00	5	.046
Maytenus rigida (Celastraceae)	1	0.005	2	0.006	4	.009
Morphospecies XVIII	2	0.002	1	0.001	2	.003
Mimosa tenuiflora (Fabaceae)	7	0.094	9	0.105	—	—
Amburana cearensis (Fabaceae)	1	0.008	2	0.147	—	—
Anadenanthera macrocarpa cf. (Fabaceae)	2	0.013	1	0.001	—	—
Lantana sp. (Verbenaceae)	2	0.019	1	0.001	—	—
Clusia paralicola (Clusiaceae)	—	—	1	0.001	100	.497
Vitex rufescens (Lamiaceae)	—	—	5	0.066	33	.452
Morphospecies IV	—	—	7	0.023	31	.076
Syagrus oleracea (Arecaceae)	—	—	17	0.647	8	.213
Simaba cuneata (Simarubaceae)	—	—	1	0.002	17	.071
Morphospecies XVI	—	—	4	0.000	11	.184
Morphospecies XIII	—	—	1	0.000	7	.076
Spondias tuberosa (Anacardiaceae)	—	—	6	0.072	1	.021
Morphospecies X	—	—	1	0.002	4	.015
Erythrina velutina (Fabaceae)	—	—	2	0.226	3	.004
Ximenia americana (Olacaceae)	—	—	2	0.002	2	.002
Morphospecies VIII	—	—	1	0.002	2	.008
Tacinga palmadora (Cactaceae)	13	0.028	—	—	2	.003
Ziziphus joazeiro (Rhamnaceae)	5	0.234	—	—	1	.001
Sideroxylon obtusifolium (Sapotaceae)	2	0.047	—	—	—	—
Morphospecies VII	—	—	2	0.128	—	—
Pilosocereus gounellei (Cactaceae)	—	—	2	0.023	—	—
Morphoespecies V	—	—	—	—	5	.019
Morphoespecies XIV	—	—	—	—	4	.005
Erythroxylum pauferrense (Erythroxylaceae)	—	—	—	—	3	.005
Morphoespecies II	—	—	—	—	2	.004
Morphoespecies XII	—	—	—	—	2	.003
Morphoespecies III	—	—	—	—	1	.003
Morphoespecies IX	—	—	—	—	1	.001
Morphoespecies XI	—	—	—	—	1	.006
Morphoespecies XVII	—	—	—	—	1	.006
Peltophorum dubium var. *adnatum* (Fabaceae)	—	—	—	—	1	.032

Note. NI = number of individuals. BA = basal area (cm).

Acknowledgments

We thank Vitor Leite Martins for logistical support for access to the study areas. We also thank Camila Santos Albuquerque, Miscilene Vitória da Silva, Marcos Medeiros Cavalcanti Júnior, Humberto de Araújo Almeida, Thallyta Guimarães de Araujo, Augusto Barbosa de Queiroz, and Sonally Cunha da Silva, among others, for their help with field activities. We thank also the reviewers for the valuable suggestions.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: We thank the Project CNPQ (Grant No. 07629-2014) for financial support.

References

Agência Executiva de Gestão das Águas do Estado da Paraíba (AESA). (2006). *Agência Executiva de Gestão das Águas do Estado da Paraíba* [Executive Agency for Water Management of the State of Paraíba]. Retrieved from http://www.aesa.pb.gov.br

Albuquerque, U. P., de Lima Araújo, E., El-Deir, A. C. A., de Lima, A. L. A., Souto, A., Bezerra, B. M., . . . Severi, W. (2012). Caatinga revisited: Ecology and conservation of an important seasonal dry forest. *The Scientific World Journal2012*(1), 19.

Alcoforado-Filho, F. G., Sampaio, E. V. S. B., & Rodal, M. J. N. (2003). Florística e fitossociologia de um remanescente de vegetação caducifólia espinhosa arbórea em Caruaru, Pernambuco [Floristic and phytosociology of arboreal deciduous thorny vegetation remnant at Caruaru, in Pernambuco]. *Acta Botanica Brasilica*, *17*, 287–303.

Alexander, J. M., Kueffer, C., Daheler, C. C., Edwards, P. J., Pauchard, A., & Seipel, T. (2011). Assembly of non-native floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 656–661.

Alvares, C. A., Stape, J. L., Sentelhas, P. C., Gonçalves, J. L. M., & Sparovek, G. (2013). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, *22*, 711–728.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*, 32–46.

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+for PRIMER: Guide to Software and Statistical Methods.* PRIMER-E. Plymouth, UK.

Angiosperm Phylogeny Group—APG IV. (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, *181*, 1–20.

Araújo, K. D., Parente, H. R., Éder-Silva, É., Ramalho, C. I., Dantas, R. T., Andrade, A. P., & Silva, D. S. (2010). Levantamento Florístico do estrato arbustivo-arbóreo em áreas contínuas de caatinga no cariri paraibano [Floristic Survey of shrubby-arboreal stratum in contiguous areas of Caatinga in the cariri of paraiba]. *Revista Caatinga*, *23*, 63–70.

Auler, A. S., Wang, X., Edwards, R. L., Cheng, H., Cristalli, P. S., Smart, P. L., & Richards, D. A. (2004). Quaternary ecological and geomorphic changes associated with rainfall events in presently semi-arid northeastern Brazil. *Journal of Quaternary Science*, *19*, 693–701.

Bernard-Verdier, M., Navas, M. L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal Ecology*, *100*, 1422–1433.

Bhat, D. M., Naik, M. B., Patagar, S. G., Hegde, G. T., Kandade, Y. G., Hegde, G. N., . . . Furtado, R. M. (2000). Forest dynamics in tropical rain forests of Uttara Kannada district in Western Ghats, India. *Current Science*, *79*, 975–985.

Bioclim. (2010). Bioclimatic variables. Retrieved from geopatial datawiki.wikidot.com/bioclim-data-sets

Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical ecology with R*. Nova York, NY: Springer.

Born, J., Pluess, A. R., Burslem, D. F. R. P., Nilus, R., Maycock, C. R., & Ghazoul, J. (2014). Differing life history characteristics support coexistence of tree soil generalist and specialist species in tropical rain forests. *Biotropica*, *46*, 58–68.

Boulangeat, I., Lavergne, S., Van, E. J., Garraud, L., & Thuiller, W. (2012). Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *Journal Biogeography*, *39*, 204–214.

Büchi, L., & Vuilleumier, S. (2014). Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. *American Society of Naturalists*, *183*, 612–624.

Carmel, Y., & Kadmon, R. (1999). Effects of grazing and topography on long-term vegetation changes in a Mediterranean ecosystem in Israel. *Plant Ecology*, *145*, 243–254.

Carnaval, A. C., Hickerson, M. J., Haddad, C. F. B., Rodrigues, M. T., & Moritz, C. (2009). Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science*, *323*, 785–789.

Carnaval, A. C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography*, *35*, 1187–1201.

Carvalho, E. C. D., Souza, B. C., & Trovão, D. M. B. M. (2012). Ecological succession in two remnants of the Caatinga in the semi-arid tropics of Brazil. *Brazilian Journal of Biosciences*, *10*, 13–19. Retrieved from http://www.ufrgs.br/seerbio/ojs/index.php/rbb/article/view/1635

Cestaro, L. A., & Soares, J. J. (2004). Variações florística e estrutural e relações fitogeográficas de um fragmento de floresta decídua no Rio Grande do Norte, Brasil [Floristic and structural variations, and the phytogeographical relationships of a deciduous forest fragment in Rio Grande do Norte State, Brazil]. *Acta Botanica Brasilica*, *18*, 203–218. Retrieved from http://dx.doi.org/10.1590/S0102-33062004000200001

Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). (2006). *Sistema Brasileiro de Classificação de Solos* [Brazilian system of soil classification]. 2nd ed. Rio de Janeiro, Brazil: Centro Nacional de Pesquisa de Solos. Retrieved from http://www.agrolink.com.br/downloads/sistema-brasileiro-de-classificacao-dossolos2006.pdf

Gariglio, M. A., Sampaio, E. V. S., Cestaro, L. A., & Kageyama, P. Y. (2010). *Uso Sustentável e Conservação dos Recursos Florestais da Caatinga* [Sustainable Use and Conservation of Caatinga Forest Resources]. Brasília, Brazil: Serviço Florestal Brasileiro. Retrieved from http://www.mma.gov.br/estruturas/sfb/_arquivos/web_uso_sustentvel_e_conservao_dos_recursos_florestais_da_caatinga_95.pdf

Hammer, O., Harper, D. T. A., & Ryan, P. D. (2001). PAST: Paleontological Statistics software package for education and data analysis. *Paleontologia Electronica*, *4*, 9.

Hauff, S. N. (2010). *Representatividade do Sistema Nacional de Unidades de Conservação na Caatinga* [Representativeness of the National System of Conservation Units in the Caatinga]. Brasília, Brazil: Programa das Nações Unidas para o Desenvolvimento. Retrieved from http://www.mma.gov.br/estruturas/203/_arquivos/representativconservcaat_shauffrevisojoo_03___produto_final_203.pdf

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., . . . O'Connor, M. I. (2012).

A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, *86*, 105–129.

Instituto Brasileiro de Geografia e Estatística (IBGE). (2012). *Manual técnico da Vegetação* [Vegetation Technical Manual]. Rio de Janeiro, Brazil. Retrieved from http://biblioteca.ibge.gov.br/visualizacao/livros/liv63011.pdf

Kessler, M. (2009). The impact of population processes on patterns of species richness: Lessons from elevational gradients. *Basic and Applied Ecology*, *80*, 295–299.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community phylogenetics and ecosystem functioning—Community assembly coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*, 592–599.

Leal, L. C., Andersen, A. N., & Leal, I. R. (2015). Disturbance winners or losers? Plants bearing extrafloral nectaries in Brazilian Caatinga. *Biotropica*, *47*, 468–474.

Leal, I. R., Silva, J. M. C., Tabarelli, M., & Lacher, T. E. (2005). Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil. *Conservetion Biological*, *19*, 701–706.

Leite, Y. L. R., Costa, L. P., Loss, A. C., Rocha, R. G., Batalha-Filho, H., Bastos, A. C., . . . Pardini, R. (2016). Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *PNAS*, *113*, 1008–1013.

Lopes, S. D. F., Schiavini, I., Oliveira, A. P., & Vale, V. S. (2011). An ecological comparison of floristic composition in seasonal semideciduous forest in Southeast Brazil: implications for conservation. *International Journal of Forestry Research*, *2012*, 1–14.

Lopes, S., Schiavini, I. S., Vale, V. S., Prado Júnior, J. A., & Arantes, S. C. (2012). Historical review of studies in seasonal semideciduous forests in Brazil: A perspective for conservation. *Brazilian Geographical Journal: Geosciences and Humanities Research Medium*, *2*, 21–40.

Lucena, R. F. P., Albuquerque, U. P., & Araújo, E. L. (2007). Does the use-value of woody plants of the Caatinga (Northeastern Brazil) explain their local availability? *Economic Botany*, *61*, 347–361.

Lucena, C. M., Lucena, R. F. P., Costa, G. M., Carvalho, T. K., Costa, G. G., Alves, R. R. N., . . . Nunes, E. M. (2013). Use and knowledge of Cactaceae in Northeastern Brazil. *Journal of Ethnobiology and Ethnomedicine*, *9*, 62.

Lucena, R. F. P., Medeiros, P. M., Araújo, E. L., Alves, G. C. A., & Albuquerque, U. P. (2012). The ecological apparency hypothesis and the importance of useful plants in rural communities from Northeastern Brazil: An assessment based on use value. *Journal of Environmental Management*, *96*, 106–115.

Manhães, A. P., Mazzochini, G. G., Oliveira-Filho, A. T., Ganade, G., & Carvalho, A. R. (2016). Spatial associations of ecosystem services and biodiversity as a baseline for systematic conservation planning. *Diversity and Distributions*, *22*, 932–943.

Martins, F. R. (1989). *Fitossociologia de florestas do Brasil: um histórico bibliográfico* [Phytosociology of Brazilian forests: A bibliographic history]. São Leopoldo. *Pesquisas*, *40*, 103–164.

McCune, B., & Grace, J. B. (2002). *Analysis of ecological communities.* MjM Software Design, Gleneden Beach, Oregon. In B. McCune, & M. J. Mefford (Eds.). *PC-ORD. Multivariate Analysis of Ecological Data*. Version 6.0. Gleneden Beach, OR: MjM Software.

McCune, B., & Mefford, M. J. (2011). *Pc-Ord version 6.0: Multivariate analysis of ecological data*. Gleneden Beach, OR: MjM Software Design.

Moro, M. F., Lughadha, E. N., de Araújo, F. S., & Martins, F. R. (2016). A phytogeographical metaanalysis of the semiarid Caatinga domain in Brazil. *The Botanical Review*, *82*(2), 91–148.

Nogués-Bravo, D., Araújo, M. B., Romdal, R., & Rahbek, C. (2008). Scale effects and human impact on the elevational taxa richness gradients. *Nature*, *453*, 216–220.

Oliveira, P. T. B., Trovão, D. M. B. M., Carvalho, E. C. D., Souza, B. C., & Ferreira, L. M. R. (2009). Florística e Fitossociologia de quatro remanescentes vegetacionais em áreas de serra no cariri paraibano [Floristic composition and phytossocioly of four vegetal remainders into mountain areas locataed in Paraiban Cariri]. *Revista Caatinga*, *22*, 169–178.

Pennington, R. T., Lavin, M., & Oliveira-Filho, A. (2009). Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 437–457.

Pereira, I. M., Andrade, L. A., Costa, J. R. M., & Dias, J. M. (2001). Regeneração natural em um remanescente de Caatinga sob diferentes níveis de perturbação, no agreste paraibano [Natural regeneration in a Caatinga fragment under different disturbance levels]. *Acta Botanica Brasilica*, *15*, 413–426.

Pereira, I. M., Andrade, L. A., Sampaio, E. V. S. B., & Barbosa, M. R. V. (2003). Use-history effects on structure and flora of Caatinga. *Biotropica*, *35*, 154–165.

Prado, D. E. (2008). *As Caatingas Da América Do Sul* [The Caatinga of South America]. In I. R. Leal, M. Tabarelli, and J. M. C. Silva (Eds.), *Ecologia e Conservação da Caatinga [Ecology and Conservation of the Caatinga]* (pp. 3–27). 3rd ed. Recife: Ed. Universitária da UFPE, Pernambuco, Brazil.

Prado-Junior, J. A., Schiavini, I., Vale, V. S., Arantes, C. S., Sande, M. T., Lohbeck, M., & Poorter, L. (2016). Conservative species drive biomass productivity in tropical dry forests. *Journal of Ecology*, *104*, 817–827.

Prance, G. T. (1982). *Biological diversification in the tropics*. New York, NY: Columbia University Press.

Queiroz, L. P. (2006). The Brazilian Caatinga: Phytogeographical patterns inferred from distribution data of the Leguminosae. In R. T. Pennington, G. P. Lewis, & J. A. Ratter (Eds.). *Neotropical savannas and seasonally dry forests: Plant diversity, biogeography and conservation* (pp. 121–157). Boca Raton, FL: CRC Press.

Quesada, M., Sanchez-Azofeifa, G. A., Alvarez-Anorve, M., Stoner, K. E., Avila-Cabadilla, L., Calvo-Alvarado, J., . . . Gamon, J. (2009). Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, *6*, 1014–1024.

Rahbek, C. (1995). The elevational gradient of species richness: A uniform pattern? *Ecography*, *18*, 200–205.

Ramirez-Marcial, N., Gonzalez-Espinosa, M., & Williams-Linera, G. (2001). Anthropogenic disturbance and tree diversity in Montane Rain Forests in Chiapas, Mexico *Forest. Ecology and Management*, *154*, 311–326.

Ramos, M. A., Ramos, M. A., & Albuquerque, U. P. (2012). The domestic use of firewood in rural communities of the Caatinga: How seasonality interferes with patterns of firewood collection. *Biomass & Bioenergy*, *39*, 147–158.

Reice, S. R. (1994). Nonequilibrium determinants of biological community structure. *American Scientist*, *82*, 424–435.

Ribeiro, E. M. S., Rodríguez, V. A., Santos, B. A., Tabarelli, M., & Leal, I. R. (2015). Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. *Journal of Applied Ecology*, *52*, 611–620.

Ribeiro, E. M. S., Rodríguez, V. A., Souza, L. G. R., & Leal, I. R. (2016). Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. *Ecology*, *97*, 1583–1592.

Rodal, M. J. N., Sampaio, E. V. S. B., & Figueiredo, M. A. (2013). *Manual sobre métodos de estudo florístico e fitossociológico—Ecossistema caatinga* [Handbook on methods of floristic and phytosociological study—Caatinga ecosystem]. 1st ed. Sociedade de Botânica, Brasília. Retrieved from http://www.botanica.org.br/ebook/man_sob_met_est_flo_fit.pdf

Sagar, R., Raghubanshi, A. S. A., & Singh, J. S. (2003). Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. *Forest Ecology and Management*, *186*, 61– 71.

Saiful, I., & Latiff, A. (2014). Effects of selective logging on tree species composition, richness and diversity in a hill dipterocarp forest in Malaysia. *Journal of Tropical Forest Science*, *26*, 188–202.

Sampaio, E. V. S. B. (1995). Overview of the Brazilian Caatinga. In S. H. Bullock, H. A. Mooney, & E. Medina (Eds.). *Seasonally tropical dry forests*. Cambridge: Cambridge University Press.

Sampaio, E. V. S. B. (2010). Características e Potencialidades [Characteristics and Potentialities]. In M. A. Gariglio, E. V. S. B. Sampaio, L. A.Cestaro, & P. Y. Kageyama (orgs.). *Uso Sustentável e Conservação dos Recursos Florestais da Caatinga* [Sustainable Use and Conservation of Caatinga Forest Resources] (pp. 29–48). Brasília, Brazil: Serviço Florestal Brasileiro.

Sanchez, M., Pedroni, F., Eisenlohr, P. V., & Oliveira-Filho, A. T. (2013). Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, Southeastern Brazil, from near sea level to 1000 m of altitude. *Flora*, *208*, 184–196.

Shepherd, G. J. (2010). *Fitopac 2.1: Manual de usuário* [User Manual]. Campinas, Brazil: Campinas, Departamento de Botânica, Universidade Estadual de Campinas.

Silva, F. K. S., Lopes, S. F., Lopez, L. C. S., Melo, J. I. M., & Trovão, D. M. B. M. (2014). Patterns of species richness and conservation in the Caatinga along elevational gradients in a semiarid ecosystem. *Journal of Arid Environments*, *110*, 47–52.

Smart, S. M., Thompson, K., Marrs, R. H., Le Duc, M. G., Maskell, L. C., & Firbank, L. G. (2006). Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceed Biological Science*, *273*, 2659–2665.

Stanley, D., Voeks, R., & Short, L. (2012). Is non-timber forest product harvest sustainable in the less developed world? A systematic review of the recent economic and ecological literature. *Ethnobiology and Conservation*, *1*, 1–39.

Tabarelli, M., Lopes, A. V., & Peres, C. A. (2008). Edge-effects drive tropical forest fragments towards an early-successional system. *Biotropica*, *40*, 657–661.

Toledo-Garibaldi, M., & Williams-Linera, G. (2014). Tree diversity patterns in successive vegetation types along an elevation gradient in the Mountains of Eastern Mexico. Ecological *Research*, *29*, 1097– 1104.

Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J. A., & Birks, H. J. B. (2010). Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography*, *19*, 810–821.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., & Beebee, T. J. C. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.

Werneck, F. P., Costa, G. C., Colli, G. R., Prado, D. E., & Sites, J. W. Jr (2011). Revisiting the historical distribution of seasonally dry tropical forests: New insights based on palaeodistribution modelling and palynological evidence. *Global Ecology and Biogeography*, *20*, 272–288.

Wiegmann, S. M., & Waller, D. M. (2006). Fifty years of change in northern upland forest understories: identity and traits of ‘‘winner’’ and ‘‘loser’’ plant species. *Biological Conservation*, *129*, 109–123.

Zhang, J., Cheng, K., Zang, R., & Ding, Y. (2014). Changes in floristic composition, community structure and species diversity across a tropical coniferous broad leaved forest ecotone. *Tropical Conservation Science*, *7*, 126–144.

Zhao, M., Pan, B., Tan, Y., & Corlett, R. T. (2015). Winners and losers among tree species in Xishuangbanna: which traits are most important? *Science Bulletin*, *60*, 916–924.